Rev. Écol. Biol. Sol, 1976, **13** (4): 595-610.

Seasonal and microstratal dietary research on *Tomocerus* (Collembola) in two forested ecosystems of eastern North Carolina

BY

Clifford B. KNIGHT

Department of Biology, East Carolina University - Greenville, North Carolina - U.S.A.

INTRODUCTION

A number of entomologists have investigated the feeding habits of various collembolans beginning with the work of MACNAMARA (1924). Based on the results of a number of research articles, it appears that forest soil collembolans are a euryphagous group of insects. As CHRISTIANSEN (1964) has stated (p. 154), « In many cases, the diet of an animals is essentially what is available. » Another investigator (VON TORNE, 1961) agreed that in its native habitat many Collembola display no selectivity with respect to nutritional material, but in the laboratory if a species is exposed to several possible diets, it will frequently display a preference. In a previous paper (KNIGHT and ANGEL, 1967) we noted that when *Tomocerus flavescens* was exposed to several nutritional choices in the laboratory, this species ingested fungal spores in preference to other food substances (*i.e.*, organic detritus and fungal hyphae).

In this study there were several problems I wished to resolve by examining the gut contents of two species of *Tomocerus (T. lamelliferus* and *T. flavescens)* throughout an annual cycle. The collection of *Tomocerus* throughout the year enabled me to compare possible seasonal and interspecific differences in nutrients ingested in two forested communities. Each sample unit at the time of removal from the forest floor was separated into an upper litter-fermentation microstratum (the A_{00} and upper portion of the A_0 horizons of a forest soil profile) and a lower humus layer (the lower portion of the A_0 horizon). Henceforth in this paper I will refer to the litter-fermentation layer as the litter layer. This subdivision of the organic soil

profile into two microstrata allowed me to compare dietary differences in each layer. The total body length of every tomoceran collected was recorded so that any dietary differences correlated with age would be apparent.

Both species were collected in the interior of two adjacent forest ecosystems. One area was dominated by sixty year old loblolly pine *(Pinus taeda)*. This community was located below a ridge line on an east facing slope. The other area contained a mixture of young hardwoods including river birch *(Betula nigra)*, sweet gum *(Liquidambar styraciflua)* and southern red oak *(Quercus rubra)*. This deciduous stand was located at a slightly lower elevation than the pine community, but on the same east-facing slope just above the flood plain of a small river.

METHODS

The two ecosystems were sampled on a bimonthly basis beginning in May, 1972 and ending in March, 1973. Three randomly chosen sample units of forest soil (each 20 cm square) were removed from each community. Every sample, at the time of removal, was separated into a litter (litter-fermentation) unit and a humus unit and placed in separate plastic bags for transport back to the laboratory. A maximum-minimum thermometer placed in the center of the sampling area of each stand recorded soil temperatures during the study period. These thermometers were positioned in the soil profile so that they actually recorded the temperature changes transpiring between the upper litter and lower humus unit. Soil moisture percentage values were calculated from samples that were oven dried in the laboratory at 105° C for 48 hours. Soil organisms were separated from the soil samples by placing them in batteries of Tullgren funnels for a 48-hour period. *Tomocerus* was isolated from sample units and stored in vials containing 95 percent ethyl alcohol prior to the analysis of gut contents.

When specimens were removed from storage vials they were placed in warm (35° C) lactic acid for three hours to clear the organism and reveal the gut and its visible contents. After clearing, each specimen was washed in distilled water and placed in a drop of warm glycerin. Each organism was measured for total body length with an ocular micrometer. After measurement, the alimentary canal was teased away from the identified specimen and opened longitudinally using glass microdissection needles. The removal and subsequent squashing of the food bolus enabled me to qualitatively and quantitatively analyze the ingested contents of the alimentary canal. Quantitative estimates were based on the system used by POOLE (1959) in which he states (p. 75) that : « ... the gut contents were examined microscopically and the total identifiable material was given the value of 10. »

RESULTS AND DISCUSSION

Two species of *Tomocerus*, *T. lamelliferus* and *T. flavescens*, were found in the litter and humus microstrata of the two vegetational communities investigated. *Tomocerus lamelliferus* was collected more frequently, making up over 74 percent of the total tomocerid fauna collected. According to the data presented in Table I, populations of *T. lamelliferus* were much larger in the coniferous area. Populations of *T. flavescens* were larger in the deciduous

community than they were in the coniferous area. The microstratification of populations of *T. lamelliferus* when based on annual totals, displayed a reversal in numbers when the two ecosystems were compared. Larger populations appeared in the upper microstratum in pine, but in the lower microstratum of the deciduous community. *Tomocerus flavescens* showed the same preponderance of specimens in the litter of coniferous communities (paralleling the distributional pattern of *T. lamelliferus* stratification in this community) but a nearly equal numerical distribution of the population occurred in the two microstrata of the deciduous area. Allogenic factors may be responsible for distributional differences in the two areas. Pine litter and humus tend to pack more tightly than comparable layers of deciduous profiles. This would tend to reduce the circulation of air and subsequent evaporation of soil moisture. But perhaps of greater importance is the fact that the tightly packed humus of a coniferous community would restrict the physical movement of *Tomocerus* through this portion of the profile. The more diffuse nature of the deciduous humus allows for easier movement through this microstratum and could conceivably account for the greater number of *T. lamelliferus* in this portion of the soil profile.

Tomocerus lamelliferus was significantly smaller (mean body length of 1.27 mm) than *T. flavescens* (mean body length of 1.64 mm). There were two peaks in mean body length recorded for *T. lamelliferus*. These were recorded in September with the greatest mean measurement of 1.58 mm recorded for the pine humus population of *T. lamelliferus*. A secondary peak in mean body length, a measurement of 1.54 mm was recorded for deciduous litter populations. The larger species *(T. flavescens)* had a peak body length value of 2.70 mm recorded in January in pine humus. The next largest mean measurement (2.65 mm) was recorded in the same month in the pine litter.

A factorial design employing analysis of variance (ANOVA) based on body length yielded significant probability values ($p < .05$) when comparing stratification and food type in pine for *T. lamelliferus* were found in the litter stratum and significantly greater numbers of these larger organisms were consuming organic detritus as their primary food source. The same test performed on organisms of *T. lamelliferus* inhabiting the deciduous community yielded no statistically significant values with regard to stratification or diet. A similar ANOVA test with *T. flavescens* yielded no significant values for the two main factors (diet and stratification) when considered separately. In the deciduous community the stratification of organisms on the basis of body length was highly significant ($p < .01$) with a greater proportion of larger organisms of *T. flavescens* located in the litter microstratum but no significant values were recorded for food type or interaction between stratification and diet.

When we compare the percentage distribution of gut contents among size classes of *Tomocerus* as shown in Figures 1 and 2, several facts are obvious. Size class 'B' (1.0 to 1.4 mm in body length) of *T. lamelliferus* is the dominant size group in both communities and both strata as is also indicated in Table II. *Tomocerus lamelliferus* probably spends a relatively short time in the early instars (body length, 0.5 to 0.9 mm) thus we find only small numbers of organisms in this size class. There is a notable decline in the numbers of *T. lamelliferus* that exceed the dominant class in size (1.5 mm

and larger). This may be the result of increased predation, because as CLARKE and GRANT (1968) have indicated, spiders prey heavily on the collembolans of the forest floor. I would assume that the larger the collembolan, the greater the chances of being consumed by a predator. Litter populations may suffer the heaviest predation pressure since the predator is more mobile in the microstratum. In fact, *T. lamelliferus* may descend into the humus stratum (where allogenic changes are damped) to molt the exoskeleton. This might explain the proportionately greater numbers of *T. lamelliferus* with no gut contents (Tab. I) in this lower microstratum. It is during this period in the life cycle that most insects are more sensitive to allogenic conditions and also more vulnerable to predatory organisms. From the standpoint of natural selection, it is possible that with lower predation pressures in the humus layer, the more successful genetic strains (successful in terms of reproductive fulfillment) generally molt in this portion of the soil profile.

TABLE I

Stratification and results of gut content analyses of *Tomocerus*. The percentage figure represents the presence of a dietary component within the gut contents. 'N' values refer to stratal population totals; 'n' values refer to specific dietary totals, *i. e.*, the number of organisms containing a specific food item.

	Fungal Derivative	Organic Detritus	Mineral Particles	No Contents
Tomocerus lamelliferus				
Pine Litter	61 %	64 %	25 %	34 %
(N = 163)	(n = 99)	(n = 104)	(n = 41)	(n = 55)
Pine Humus	29 %	45 %	14 %	51 %
(N = 78)	(n = 23)	(n = 35)	(n = 11)	(n = 40)
Decid. Litter	57 %	70 %	11 %	25 %
(N = 47)	(n = 27)	(n = 33)	(n = 5)	(n = 12)
Decid. Humus	29 %	45 %	23 %	54 %
(N = 80)	(n = 23)	(n = 36)	(n = 18)	(n = 43)
Tomocerus flavescens				
Pine Litter	41 %	47 %	12 %	47 %
(N = 34)	(n = 14)	(n = 16)	(n = 4)	(n = 16)
Pine Humus	56 %	56 %	0 %	44 %
(N = 9)	(n = 5)	(n = 5)	(n = 0)	(n = 4)
Decid. Litter	49 %	47 %	21 %	47 %
(N = 47)	(n = 23)	(n = 22)	(n = 10)	(n = 22)
Decid. Humus	20 %	40 %	23 %	58 %
(N = 40)	(n = 8)	(n = 16)	(n = 9)	(n = 23)

Another point is that fungal material appears in proportionately greater amounts in larger size classes (more mature individuals) as compared with organic detritus or individuals lacking gut contents in *T. lamelliferus* (Fig. 1). We might wonder whether this is due to changes in nutritional demands as the organism matures or whether it might be an accidental circumstance that

happened to occur independently on four separate occasions (each microstratum displays the same general trend). If it does reflect a nutritional requirement, perhaps it might be associated with reproductive development, though this is all pure speculation at this stage of scientific inquiry. No such patterns are apparent for *T. flavescens* where much smaller populations and a greater number of size classes (Fig. 2 and Tab. II) tend to obscure distri-

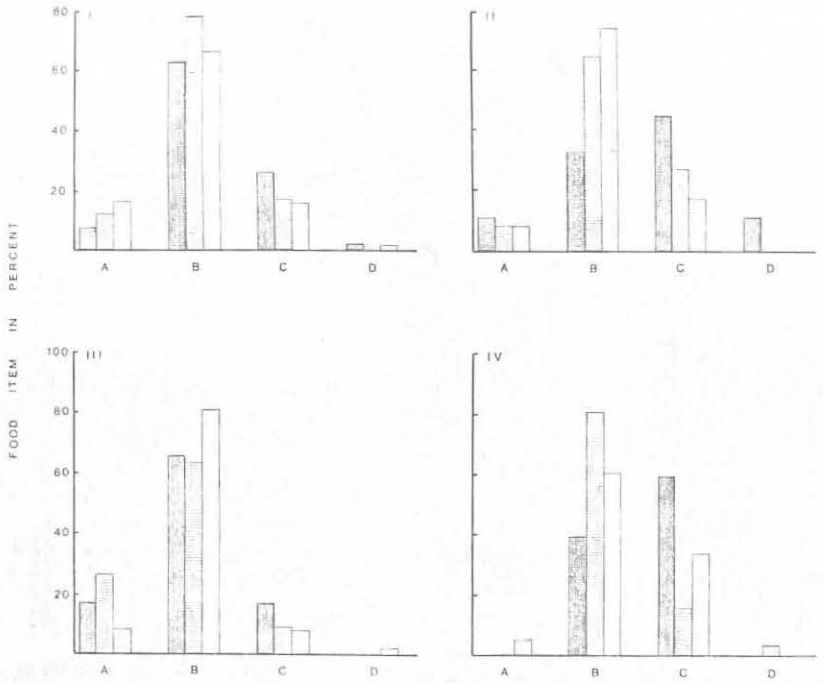

FIG. 1. — The percentage distribution of gut contents for each size class of *T. lamelliferus* is represented for each microstratum and community investigated. Cross hatched bars indicate fungal derivatives as the main diet, horizontally lined bars indicate organic detritus as the main diet and open bars indicate no gut contents. Size classes are as follows : A = 0.5 to 0.9, B = 1.0 to 1.4, C = 1.5 to 1.9, D = 2.0 to 2.4 mm. Graph I represents pine litter ; Graph II represents deciduous litter ; Graph III represents pine humus ; Graph IV represents deciduous humus.

butional trends. Though *T. lamelliferus* tends to follow a normal curve of distribution (slightly skewed), *T. flavescens* exhibits a platykurtic distribution of size classes in both microstrata of pine and atypical distributional patterns in the deciduous area.

On an annual distributional basis, when bimonthly collections and type of diet (fungal material versus organic detritus) are used as the main factors in an ANOVA test, diet type, bimonthly distribution and interaction yield highly significant values ($p < .01$) for *T. lamelliferus*. As indicated in Figure 3, organic detritus with few exceptions is the visible foodstuff that dominates gut contents in both communities and in each microstratum in this trivial group of springtails. But the much smaller populations of *T. flaves-*

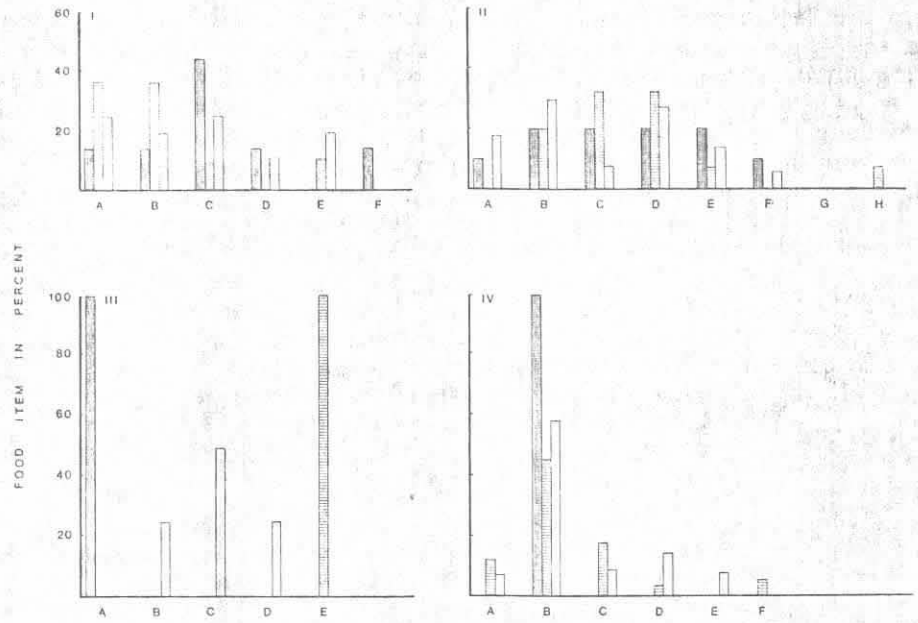

FIG. 2. — The percentage distribution of gut contents for each size class of *T. flavescens* is represented for each microstratum and community investigated. Cross hatched bars indicate fungal derivates as the main diet, horizontally lined bars indicate organic detritus as the main diet and open bars indicate no gut contents. Size classes are as follows : A = 0.5 to 0.9, B = 1.0 to 1.4, C = 1.5 to 1.9, D = 2.0 to 2.4, E = 2.5 to 2.9, F = 3.0 to 3.4, G = 3.5 to 3.9, H = 4.0 to 4.4 mm. Graph I represents pine litter ; Graph II represents deciduous litter, Graph III represents pine humus, Graph IV represents deciduous humus.

TABLE II

The percentage distribution of the various size classes of *T. lamelliferus* and *T. flavescens* in all the microstrata investigated

	Total Body Length in mm							
	0.5-0.9	1.0-1.4	1.5-1.9	2.0-2.4	2.5-2.9	3.0-3.4	3.5-3.9	4.0-4.4
T. lamelliferus								
Pine Litter.....	13 %	68 %	18 %	1 %				
Pine Humus.....	17 %	73 %	9 %	1 %				
Deciduous Litter.....	8 %	63 %	27 %	2 %				
Deciduous Humus....	2 %	68 %	29 %	1 %				
T. flavescens								
Pine Litter.....	26 %	23 %	23 %	12 %	12 %	4 %		
Pine Humus.....	34 %	11 %	22 %	11 %	22 %			
Deciduous Litter.....	10 %	23 %	19 %	29 %	13 %	4 %		2 %
Deciduous Humus....	10 %	55 %	13 %	15 %	5 %	2 %		

cens (Fig. 4), when compared on the same statistical basis, present no such statistically significant values for either coniferous or deciduous areas.

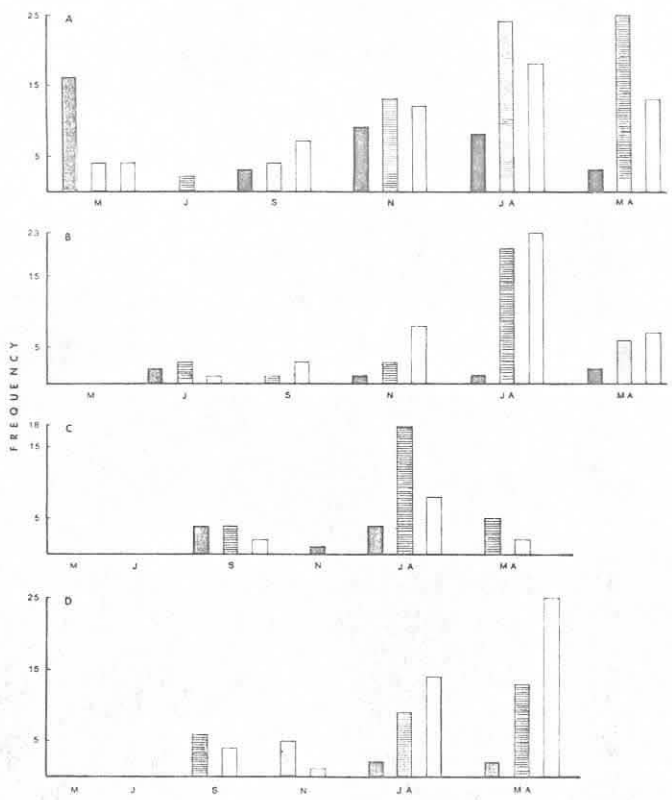

FIG. 3. — A bimonthly frequency histogram showing the microstratal distribution of *T. lamelliferus* in both ecosystems ; graph A (pine litter), graph B (pine humus), graph C (deciduous litter), graph D (deciduous humus). Along the abscissa the following letters represent the months indicated: M (May), J (July), S September), N (November), JA (January), and MA (March). Dietary symbols are the same as those in Figs. 1 and 2.

Gut content analyses of *T. lamelliferus* and *T. flavescens* indicated the existence of three visible dietary items in both species (Tab. I). There were (1) fungal derivatives (including hyphae, conidial parts, spores), (2) organic detritus made up of macerated bits of plant debris (one of the chief constituents of litter and humus layers of the forest floor) and (3) mineral particles. Particles of ingested material were measured using an ocular micrometer at the time the food bolus was examined. Hyphal pieces varied in length from 0.03 to 0.80 mm, but most pieces averaged 0.05 mm. The diameter of these hyphal segments ranged from 0.003 to 0.05 mm with a mean diameter of 0.005 mm. Spore diameter measurements ranged from 0.005 mm to 0.01 mm. Mineral particles which appeared quite frequently, particularly when large quantities of organic detritus were found in the gut ranged from

a diameter of 0.005 mm to 0.06 mm with a mean diameter of 0.03 mm. All mineral particles were irregular in shape, but diameter measurements should be interpeted as the distance along the greatest axis. All mineral particles found within the gut contents of both species were clear, crystalline quartz (silicon dioxide).

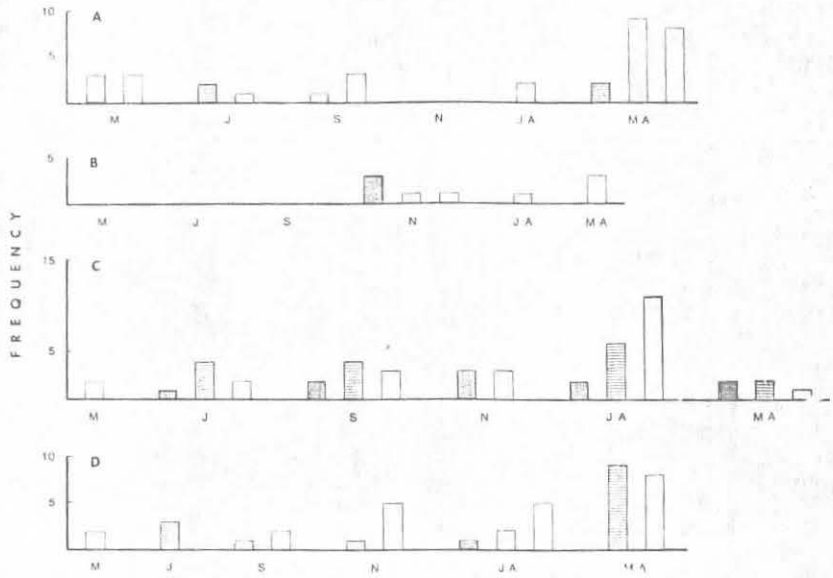

FIG. 4. — A bimonthly frequency histogram showing the microstratal distribution of *T. flavescens* in both ecosystems ; graph A (pine litter), graph B (pine humus), graph C (deciduous litter), graph D (deciduous humus). Along the abscissa the following letters represent the months indicated : M (May), J (July), S (September, N (November), JA (January), and MA (March). Dietary symbols are the same as those in Figs. 1 and 2.

Some of the collected organisms had apparently empty digestive tracts, which according to some authors (POOLE, 1959; CHRISTIANSEN, 1964) may mean that these individuals are ingesting bacteria which would not be visible under the light microscope without special stains. I do not question the possibility that bacteria may serve as a valuable food source for some collembolans as GISIN (1952) had indicated years ago,, but I am inclined to agree with ANDERSON and HEALEY (1972). They believe that it is unlikely that large entomobryids would ingest bacteria without also consuming some plant material as an accidental inclusion. This would seem to rule out the possibility that these larger collembolans *(Tomocerus)* with no visible contents would be feeding only on bacteria. Anderson and Healey believe that soil collembolans enter non-feeding periods that are associated with molting activity.

BÖDVARSSON (1970) while studying the dietary habits of seven species of soil Collembola of southern Sweden agreed that empty digestive tracts meant that either molting activity had voided the gut or lactic acid treatment rendered the gut contents invisible. This latter suggestion would seem highly unlikely unless the gut were retaining only minute amounts of ingested mate-

rial. The forementioned hypotheses would lead to the following four possibilities: that *Tomocerus lamelliferus* and *T. flavescens* (1) depend solely on bacterial organisms that are ingested with surrounding organic detritus and fungal matter, (2) obtain their nutrients from absorption of both organic detritus, fungal material and bacteria. In other words, all ingested organic matter contributes to the overall nutrient availability of these arthropods. Another alternative is that (3) only visible organic matter functions as a prime nutrient source with the implication that fungal products and organic detritus are both important contributors in a nutritional sense. Finally, the last alternative is that (4) either fungal derivatives or organic detritus functions as the primary nutritional source with other materials playing a supplementary but unnecessary role in the organism's diet. The first possibility would not preclude the supposition that visible contents might be acting as a transporting agent for the bacterial materials that are actually absorbed through the gut wall. If this hypothesis is correct, much of the visible matter is functioning in conveyor-belt fashion, introducing a rich store of bacterial material into the alimentary canal of the organism for subsequent absorption. Personally, until more sophisticated techniques are available, I am inclined to favor the second possibility.

Based on my observations, I am inclined to agree with CHRISTIANSEN (1964) when he states (p. 155) that, « ... it is more than probable that digestion, at least in soil Collembola, is a cooperative venture; food material passes through the digestive tracts of many individuals, and under the influence of bacteria, fungi, and the several sets of digestive enzymes becomes more and more utilizable. » I have noted that along the entire gut area certain contents appear unchanged from the foregut region until they are eliminated as fecal pellets as GILMORE (1970) has noted. But along with these apparently unaltered materials there were other pieces of hyphae and spores that had been altered in a structural way. That is, the cell walls of the hyphae and spores had begun to exhibit indications of breakdown. Certain pieces of hyphae contained vesicular enlargements along the cell wall, an indication that possible enzymatic activity was initiating a breakdown of cytological structures. This fact coupled with the changes in color and density, leads me to believe that decomposition and eventual piecemeal absorption of nutrients is dependent upon repetitive passage of fungal and detrital matter through the gut of many forest floor detritivores. Very frequently I found hyphal segments along different portions of the gut (or even in the same portion of the digestive tract) exhibiting a varying color density from a very dark brown to a totally transparent (colorless) segment. Yet the optical density had nothing to do with position in the tract. That is, dark brown pieces were frequently found in a fecal pellet about to be egested and colorless chunks of hyphae were located in a number of cases near the anterior end of the tract. This would seem to imply repetitive ingestion (coprophagy), with each passage probably relinquishing a certain quantity of nutrient material.

In Table I, there appears to be an indication of a feeding pattern exhibited by *T. lamelliferus* in both vegetational areas. This species had greater percentages of individuals with fungal and detrital contents in the upper litter microstratum and higher percentages of individuals with empty guts or invi-

sible contents in the humus microstratum. This would seem to imply that more active feeding occurs in the upper portion of the organic profile. At the same time we might also conclude that molting and other non-feeding activities occur in the humus layers of both ecosystems. *Tomocerus flavescens* exhibited the same trends (Tab. I) in the deciduous area, but a complete reversal of this patterns was observed in organisms sampled from the pine stand. Two possibilities might explain this atypical pattern of feeding behavior by *T. flavescens* in the coniferous community. There might, in fact, be a reversal of roles for this species in the pine stand, or the population in this type of community (43 organisms of all age groups in pine as compared with 87 organisms of all age groups in the deciduous area) may not be large enough to give a valid view and instead we are observing an extremely limited and distorted pattern of distribution and niche.

Fungal derivatives (hyphae, spores, conidia) are not a universal constituent of visible gut contents as one will note in Table I and Figures 1 through 4. Though 61 percent of *T. lamelliferus* collected from pine litter contained fungal derivatives (the highest percentage in any microstratum for either species), this percentage is based on the mere existence of this material within the gut and not its quantitative contribution to the total contents. In fact, in many instances if fungal matter was present, it was only a minor inclusion. In spite of statements by other workers (SCHALLER, 1949; POOLE, 1959) implying that soil fungi are the most important dietary element, I am inclined to agree with BÖDVARSSON (1970) when he asserts that fungal hyphae are not as common in the gut as the past literature would lead one to believe. Amorphous material (organic detritus) he states is always a conspicuous ingredient of gut contents. Certainly this is evident when we examine Figures 3 and 4. In these graphs the dominant dietary component is represented for *T. lamelliferus* in pine (graphs A and B) and deciduous communities (graphs C and D). In only two instances did fungal derivatives exceed organic detritus (pine litter in May and deciduous litter in November).

But despite the apparent tendency among members of the two trivial groups investigated *(T. lamelliferus* and *T. flavescens)* to ingest large quantities of organic detritus, splitting the two populations into distinct size classes as shown in Table III and IV suggests a dietary trend for *T. lamelliferus* in one ecosystem. When the dominant food item within the gut was considered, note that in both microstrata of the pine ecosystem (Tab. III) the fungal component increased with increasing body length (age). A statistical test of correlation comparing the relative amount of fungal material with body length yields a positive correlation with a statistically significant probability in pine litter ($p < .01$) and in pine humus ($p < .05$). In spite of this increase in fungal material with increasing age in pine, no such trend was apparent in the deciduous area. Similar patterns of dietary change were not the case for *T. flavescens*; perhaps populations of *T. flavescens* were not large enough to display a trend.

The presence of mineral particles (small grains of quartz) in the gut contents of *Tomocerus* in every microstratum (Tab. I) can probably be considered an accidental inclusion. All of these particles were similar in that they were all irregular in shape and were grains of quartz. It is doubtful that they served any digestive function. As POOLE (1959) indicated in one

of his tables, these particles were present in trace quantities, rarely exceeding 5 percent of the total contents. Their only conceivable function in my opinion would have been a means by which the organic contents might have been physically macerated.

TABLE III

The number of organisms of *T. lamelliferus* and size classes with either fungal derivatives or organic detritus as the dominant dietary item. The proportionate number of organisms with organic matter in the gut is represented as a percentage value. Numbers in parentheses represent the total number of organisms within that microstratum.

	Total Body Length in mm			
	0.5-0.9	1.0-1.4	1.5-1.9	2.0-2.4
Pine Litter				
Fungal Derivative	23 %	33 %	50 %	100 % (1)
Organic Detritus	77 %	67 %	50 %	
Pine Humus				
Fungal Derivative	10 %	16 %	25 %	
Organic Detritus	90 %	84 %	75 %	
Deciduous Litter				
Fungal Derivative	33 %	14 %	36 %	100 % (1)
Organic Detritus	67 %	86 %	64 %	
Deciduous Humus				
Fungal Derivative		7 %	16 %	
Organic Detritus		93 %	84 %	100 % (1)

A factorial ANOVA design was computed to determine whether there was a statistically significant distribution of the two species (based on population size) with respect to microstrata, a difference in the type of food ingested and in interaction between stratification and food ingestion. *Tomocerus lamelliferus* was found in the upper litter microstratum in significantly greater numbers ($p < .05$) in the pine stand. More members of the species consumed significantly greater quantities of organic detritus than fungal material when we include the entire population in our calculations. But in the deciduous area, there was no statistically significant differences in stratification or dietary choice despite the greater number of organisms ingesting organic detritus. *Tomocerus flavescens*, according to collecting results, had much smaller populations in both communities. In pine, this species displayed no significant differences in stratification or food choice, however an interaction between stratification and diet was highly significant ($p < .01$). In the deciduous area, *T. flavescens* had significantly higher populations in the litter layer ($p < .01$) of the forest floor, but there was no statistical significance when diets were compared or interaction between stratification and diet.

TABLE IV

The number of organisms of *T. flavescens* and size classes with either fungal derivatives or organic detritus as the dominant dietary item. The proportionate number of organisms with organic matter in the gut is represented as a percentage value. Numbers in parentheses represent the total number of organisms within that microstratum.

	Total Body Length in mm							
	0.5-0.9	1.0-1.4	1.5-1.9	2.0-2.4	2.5-2.9	3.0-3.4	3.5-3.9	4.0-4.4
Pine Litter								
Fungal Derivative....	20 %	20 %	75 %	50 %		100 % (1)		
Organic Detritus.....	80 %	80 %	25 %	50 %	100 % (1)			
Pine Humus								
Fungal Derivative....	100 %							
Organic Detritus.....					100 % (2)			
Deciduous Litter								
Fungal Derivative....	100 %	40 %	28 %	25 %	67 %	100 % (1)		
Organic Detritus.....		60 %	72 %	75 %	33 %			100 % (1)
Deciduous Humus								
Fungal Derivative....		13 %						
Organic Detritus.....	100 %	87 %	100 %	100 %		100 % (1)		

A factorial ANOVA design comparing diet and bimonthly distribution in both communities yielded statistically significant results for diet type ($p < .01$), bimonthly distribution ($p < .01$) and interaction between diet and bimonthly distribution ($p < .01$) for *T. lamelliferus*. In this species, organic detritus occurred in a significantly greater number of springtails and a significantly greater number of organisms were collected during the November, January and March sampling periods. It was during these periods that temperatures tended to decline and moisture values were somewhat less extreme (Fig. 5 and 6). The lower rate of evaporation (a result of lower temperatures) could have conceivably retarded the drying of organic detritus perhaps making it more palatable and it would have favored increased fungal growth. These factors could have resulted in an increase in feeding activity of the population during this annual interval. A similar ANOVA design for *T. flavescens* yielded no statistically significant values for diet type or bimonthly distribution. The fact that no significant results materialized for *T. flavescens* could have been the result of much smaller populations of *T. flavescens* in both areas throughout the collecting cycle.

The fact that I found two species of *Tomocerus* occupying the same microstrata and feeding on identical foods would apparently refute the concept of competitive exclusion or the inability of two species to occupy the same ecological niche. Several papers in the past few years have noted this same fact (GILMORE and RAFFENSBERGER, 1970; MCMILLAN and HEALEY, 1971;

ANDERSON and HEALEY, 1972). I believe that as we continue to investigate the decomposer food chain in various ecosystems we will find that detritivores in different trivial categories may occupy the same niche. It would seem probable since the energy source for these organisms is plentiful and conse-

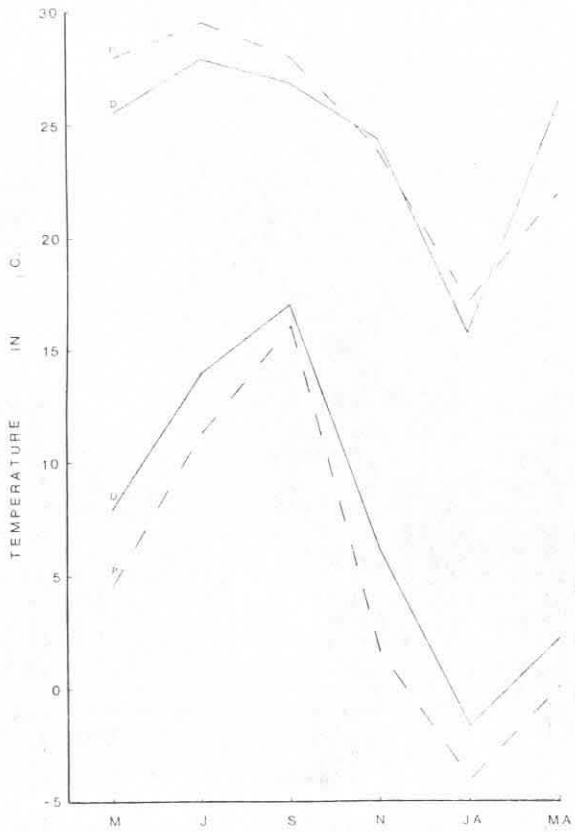

FIG. 5. — Maximum-minimum temperatures recorded in both ecosystems throughout the collecting period. Dashed lines labelled 'P' represent temperatures recorded for pine, solid lines labelled 'D' are for the deciduous ecosystem.

quently would alleviate the specter of competition. The fact that extraction of energy probably becomes a cooperative effort as CHRISTIANSEN asserted requiring repetitive ingestion of organic substances to insure proper breakdown by populations (and probably by interspecific aggregations) would tend to increase the likelihood of combined effort rather than the competitive exclusion that apparently characterizes the consumer food chain. Though we find the niche concept is an apparently valid hypothesis for consumer food webs, it appears to be untenable as we examine certain detritivore groups. Such conclusions should not perturb ecologists or biologists in general,

because biology is a science that deals with dynamic entities implying that a change of viewpoint and exceptions will come to pass as we extend our scientific frontiers.

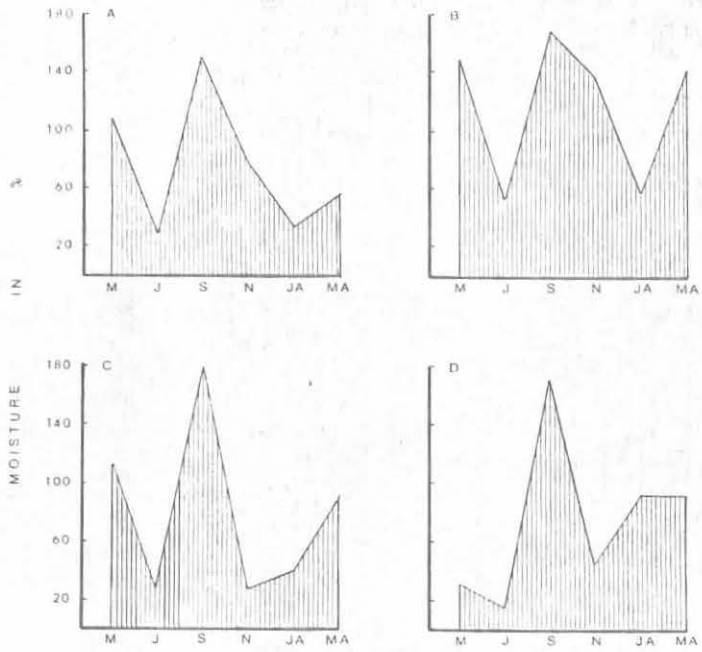

FIG. 6. — Moisture percentage values are based on oven-dry weight of litter and humus microstratal samples. Samples were collected on a bimonthly basis. Letters along the abscissa represent the following months: M - May, J - July, S - September, N - November, JA - January, MA - March. Graph A represents the moisture values in pine litter, graph B in pine humus, graph C in deciduous litter and graph D in deciduous humus.

SUMMARY

The feeding habits of two species of *Tomocerus*, *T. lamelliferus* and *T. flavescens*, were traced throughout an annual cycle by examining the gut contents. The two trivial groups were collected from the litter-fermentation and humus microstrata of a loblolly pine and a mixed deciduous community. Three random samples (20 cm square) of the upper soil profile were removed from each ecosystem on a bimonthly basis.

Tomocerus lamelliferus was the smaller and more common species. Gut content analyses of both species indicated the inclusion of organic detritus, fungal derivatives and mineral particles as normal dietary fare. *Tomocerus lamelliferus* was found in statistically significant numbers in the litter microstratum (as compared with the humus layer) of the pine community and organic detritus was consumed in significantly greater quantity than fungal material. But no statistically significant results were obvious from data collected from the deciduous area, though deciduous humus populations of the species were larger

than those recovered from the upper (litter) microstratum. There was a tendency for larger (older) members of *T. lamelliferus* to ingest fungal material with greater frequency in both microstrata and each ecosystem investigated.

Tomocerus flavescens was distributed so sparsely in both communities that no statistically significant evaluations are possible. It would appear that feeding activity occurs more frequently in the litter microstratum of the soil profile and the humus microstratum may serve as a convenient refuge for molting activity when the organism would be more vulnerable to predation.

Résumé

On a observé la manière dont se nourrissent habituellement les deux espèces de *Tomocerus*, le *T. lamelliferus* et le *T. flavescens*, à travers un cycle annuel, en examinant le contenu de leur appareil digestif. Ces deux groupes triviaux proviennent de la fermentation de matières organiques de la couche supérieure (litière) du sol et des microstrates de l'humus d'un pin loblolly et d'un groupe mixte d'arbres à feuilles caduques. On a pris trois échantillons (de 20 cm²) au hasard, dans le profil supérieur du sol de chaque ecosystème tous les deux mois.

Le *Tomocerus lamelliferus* était l'espèce la plus petite et la plus commune. Les analyses du contenu de l'appareil digestif des deux espèces ont montré la présence de détritus organiques, de dérivés de fongus et de particules minérales, comme faisant partie de leur nourriture habituelle. On a trouvé un nombre significatif de *Tomocerus lamelliferus* dans la microstrate des matières organiques de la couche supérieure du sol (différent en cela de la couche de l'humus) sous les pins, et la consommation de détritus organiques était plus importante que celle des dérivés de fongus. Mais statistiquement on n'a pas pu obtenir de résultats significatifs des matériaux rassemblés sous les arbres à feuilles caduques, bien que la population des espèces trouvées dans l'humus des arbres à feuilles caduques fût plus important que celle de la microstrate des matières organiques de la couche supérieure du sol. Les membres les plus grands (les plus âgés) de *Tomocerus lamelliferus* avaient tendance à ingérer plus fréquemment les matériaux dérivés de fongus dans les deux microstrates et chaque écosystème analysé.

Le *Tomocerus flavescens* était en si petit nombre dans les deux groupes d'arbres qu'il n'a pas été possible d'en évaluer le nombre de manière significative. Il apparaît que les activités concernant la nourriture sont plus fréquentes dans la microstrate des matières organiques de la couche supérieure d'un profil du sol et que la microstrate de l'humus peut servir à point nommé de refuge pour la mue, quand l'organisme est plus vulnérable à la prédation.

Acknowledgements

I am grateful to Mrs. Carol Lunney for her helpful comments and the reproduction of graphic material.

References

Anderson (J. M.) and Healey (I. N.), 1972. — Seasonal and interspecific variation in major components of the gut contents of some woodland Collembola. *J. Animal Ecol.*, **41**: 359-368.

BÖDVARSSON (H.), 1970. — Alimentary studies of seven common soil-inhabiting Collembola of southern Sweden. *Ent. Scand.*, **1**: 74-80.

CHRISTIANSEN (K.), 1964. — Bionomics of Collembola. *Ann. Rev. Ent.*, **9**: 147-178.

CLARKE (R. D.) and GRANT (P. R.), 1968. — An experimental study of the role of spiders as predators in a forest litter community. Part 1. *Ecology*, **49**: 1152-1154.

GILMORE (S. K.), 1970. — Collembola predation on nematodes. *Search - Agric., Cornell Univ. Exp. Sta.*, **1**: 1-12.

GILMORE and RAFFENSBERGER (E. M.), 1970. — Foods ingested by *Tomocerus* spp. (Collembola, Entomobryidae), in relation to habitat. *Pedobiologia*, **10**: 135-140.

GISIN (G.), 1952. — Oekologische Studien uber die Collembolen des Blattkomposts. *Rev. Suisse Zool.*, **59**: 543-578.

KNIGHT (C. B.) and ANGEL (R. A.), 1967. — A preliminary study of the dietary requirements of *Tomocerus* (Collembolla). *Amer. Midl. Natur.*, **77**: 510-517.

MACNAMARA (C.), 1924. — Food of Collembola. *Can. Entomol.*, **56**: 99-105.

MCMILLAN (J. H.) and HEALEY (I. N.), 1971. — A quantitative technique for the analysis of gut contents of Collembola. *Rev. Écol. Biol. Sol*, **8**: 295-300.

POOLE (T. B.), 1959. — Studies on the food of Collembola in a Douglas fir plantation. *Proc. Zool. Soc. London*, **132**: 71-82.

SCHALLER (F.), 1950. — Biologische Beobachtungen an humusbildenden Bodentieren, inbesondere an Collembolen. *Zool. Jb. (Syst.)*, **78**: 506-525.

TORNE (E. von), 1961. — Ökologische Experimente mit *Folsomia candida* (Collembola). *Pedobiologia*, **1**: 146-419.